The Genus Riella, with Descriptions of new Species from North America and the Canary Islands*

By M. A. Howe and L. M. Underwood

(With Plates 11 and 12)

The genus *Riella* occupies a unique position among the Hepaticae. The striking peculiarities of its gametophytic phase have attracted the attention of such morphologists as Hofmeister, Leitgeb, and Goebel, in addition to the interest excited among those who have devoted themselves more exclusively to a study of the systematic relations of the Hepaticae. *Riella helicophylla*, an Algerian species, is alluded to in some of the standard botanical text-books as being peculiar among the liverworts in having a leaf-like lamina or wing disposed spirally in relation to the axis or stem. Later studies of this species, however,† indicate that the supposed helicoid spiral arrangement was exaggerated in the original figures and description and that the spiral appearance is due to the slight torsion of a stem bearing a strongly undulate lamina. Nevertheless, the species of *Riella* in general are peculiar enough in that the lamina or wing appears at first sight to be attached to one side of the stem; but the position of the sexual organs, of the root-hairs and of the scale-like appendages shows that the plant is bilaterally symmetrical in the plane of the wing and the conviction is now general that the wing is dorsal in relation to the stem. Goebel‡ has expressed the opinion that the chief difference between *Riella* and the other liverworts is that in *Riella* the development of the thallus is in the vertical instead of in the horizontal plane. The species of *Riella* are all aquatic, commonly growing entirely submerged, and it is doubtless this condition of growth which makes possible the leading peculiarity in form.

The growing point of a young plant or of a young branch of

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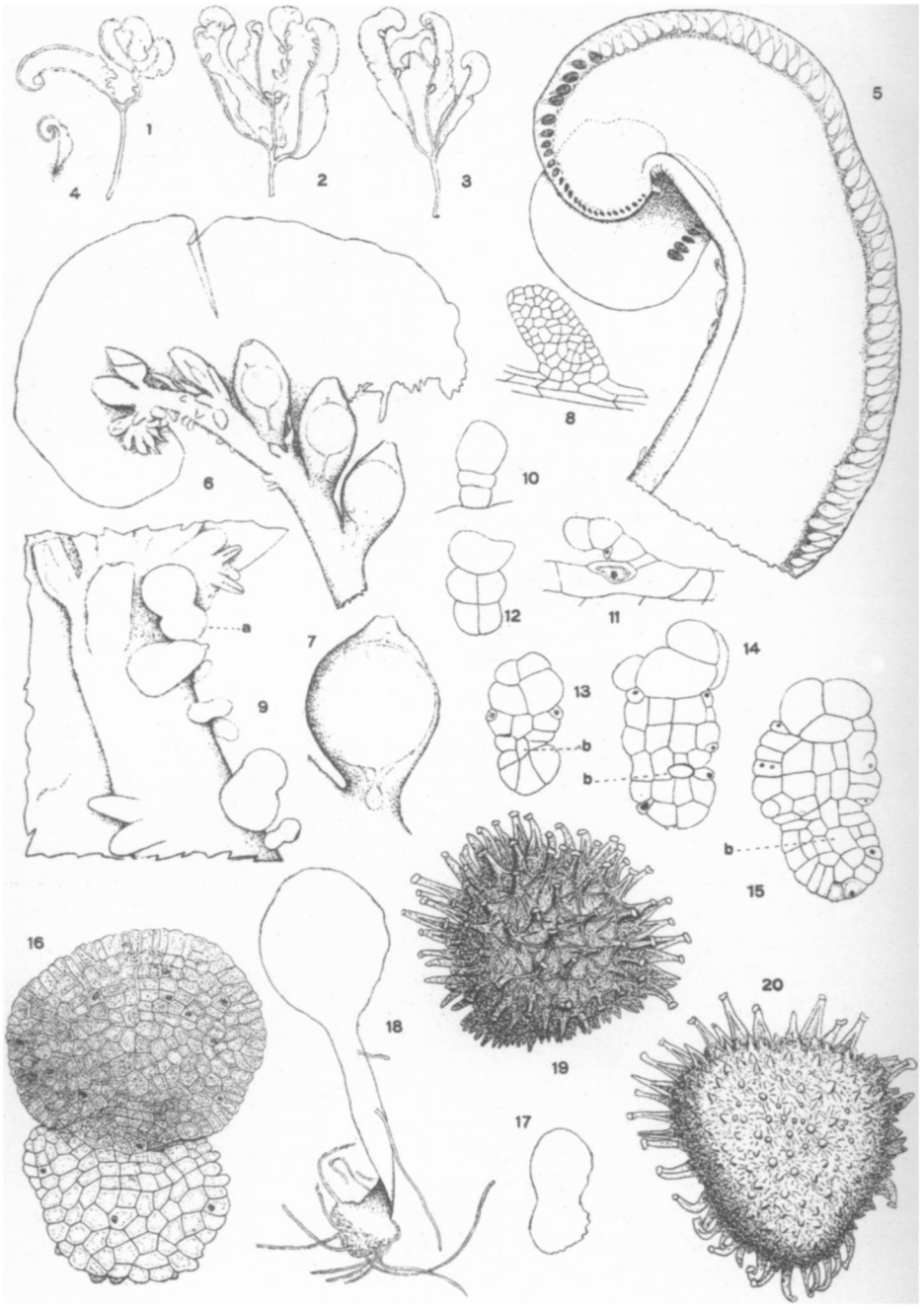
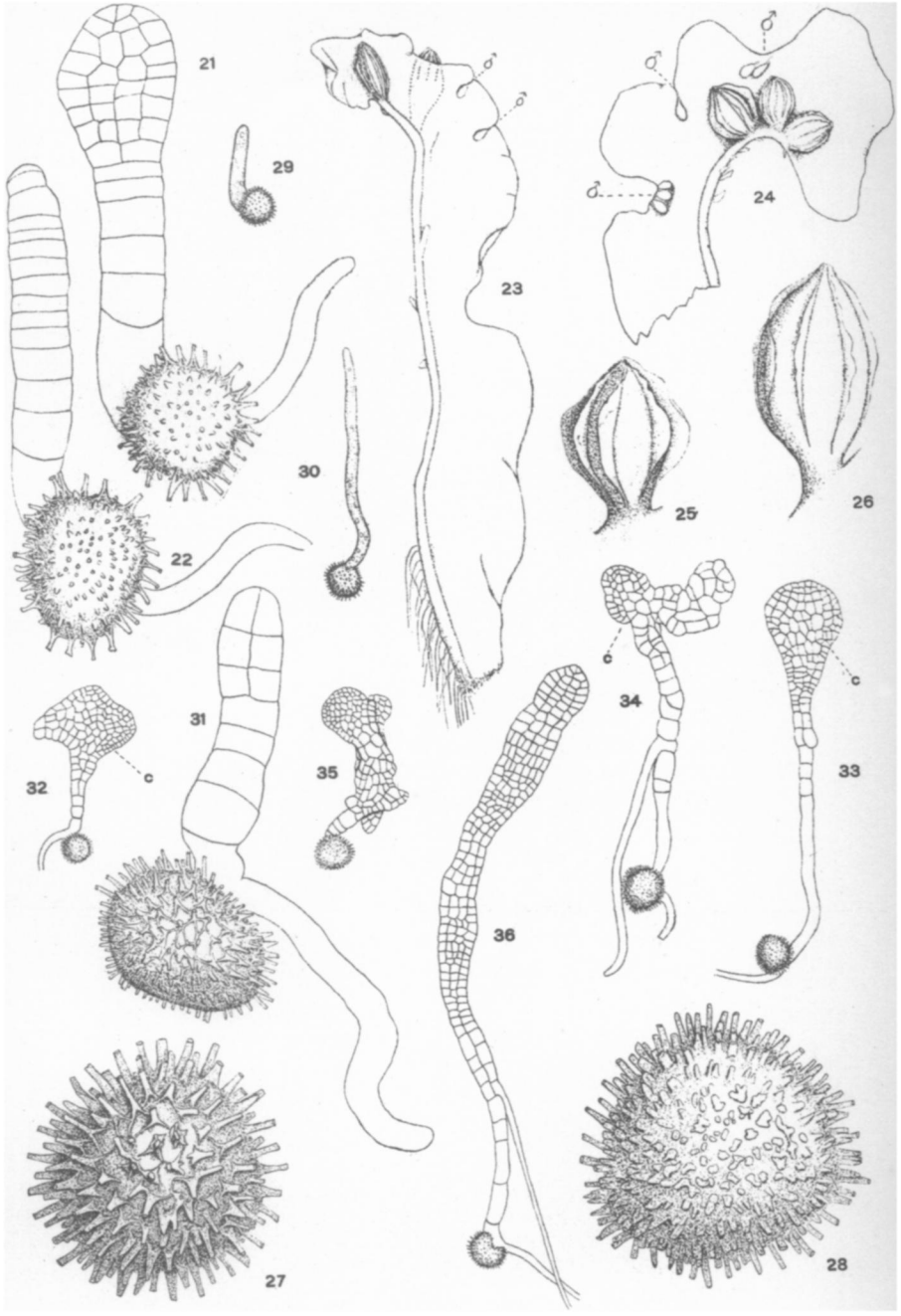
† Trabut, Rev. Gén. Bot. 3: 451. 1891. Stephani, Bull. Herb. Boiss. 7: 659. 1899.

‡ Flora, 77: 107. 1893.



RIELLA AMERICANA Howe & Underw.



21 and 22. RIELLA AMERICANA Howe & Underw.

23-36. RIELLA AFFINIS Howe & Underw.

Riella is not apical in the ordinary sense of the word, but intercalary. The whole tissue of the young shoot appears to be meristematic at first and of one layer of cells. Later, the growth activities are concentrated at either one or two points on the margin of the shoot intermediate between its distal and proximal extremities. If at *two* points, these are situated on opposite margins of the shoot. The new cells formed on the upper or distal side of the growing point now contribute to the growth of the unistratose wing, which is dorsal in position. The new cells formed on the lower or proximal side of the growing point go to constitute the multistratose stem, which is ventral in position. If two growing points on opposite margins of a young shoot persist, a double or twin plant is formed, the two branches of the axis bearing a single continuous dorsal wing. If, however, only one growing point persists, the plant or branch is apparently one-sided, with stem on one side and wing on the other, though in reality the wing is dorsal and the stem ventral.

On account of the absence of elaters, *Riella* was at first placed with the Ricciaceae, together with *Sphaerocarpus*, in which, likewise, elaters are not developed. A better understanding of the morphology of these two genera has led to placing them in the order Jungermanniales, of which, together with the exclusively American genus *Thallocarpus*, they constitute the simplest members. The genus *Riella* forms the subfamily Rielloideae and in the usual arrangement stands between the Sphaerocarpoideae and Metzgerioideae in the family Metzgeriaceae (the Jungermanniaceae anakrogynae of Leitgeb and Schiffner).

The geographical distribution of this strongly characterized genus *Riella* is of interest. Up to within a few months ago, the genus was supposed, as far as the literature on the subject is concerned, to be confined to the Mediterranean drainage basin of Africa and Europe, with seven species, as commonly recognized. One of these, however, *Riella Gallica*, was reduced by M. Corbière in the last number of the Revue Bryologique for 1902 to forma *Gallica* of the Algerian *R. Battandieri*. To these seven known species, or six, as now conceived, another from a region far removed was added by Morten P. Porsild in a recent number of the Botanisk Tidsskrift, where *R. Paulsenii* from Turkestan was

described and figured. References to the principal literature dealing with the genus, together with the names and distribution of the species hitherto described, are given below:

RIELLA Mont. Ann. Sci. Nat. III. **18**: 11. 1852. Leitgeb, Untersuch. Leberm. **4**: 74–87. *pl. 7, 8. f. 1–8.* 1879. Trabut, Rev. Gén. Bot. **3**: 449. 1891. Goebel, Flora, **77**: 104–108. *pl. 2. f. 1–3.* 1893. Schiffn.; E. & P. Nat. Pflanzenfam. **1**[3]: 51. 1893. Stephani, Bull. Herb. Boiss. **7**: 658. 1899.

Duriaea Bory & Mont. Compt. Rend. Hebd. Acad. Sci. **16**: 1115. 1843; Ann. Sci. Nat. III. **1**: 228. 1844. G. L. & N. Syn. Hep. 593. 1846. Not *Durieua* Mérat, Mém. Soc. Roy. Sci. Lille, **1827–28**: 432. 1829. Not *Durieua* Boiss. & Reut. Diag. Pl. Nov. Hisp. 14. 1842.

Maisonneuvea Trevis.* Mem. R. Ist. Lomb. III. **4**: 442. 1877.

Duriella Clauson & Billot, *fide* Schiffn., *l. c.*

RIELLA BATTANDIERI Trab. Rev. Bryol. **13**: 35. *pl. 3.* 1886. Schiffn. Bot. Centralb. **27**: 240. *pl. 1. f. 5.* 1886.

ALGERIA: Maison-Blanche near Algiers, *Battandier, Trabut.*

EXSICC.: Husnot, Hep. Gall. no. 173.

Forma GALLICA (Bal.) Corbière, Rev. Bryol. **29**: 113. 1902.

Riella Gallica Bal.; Trab. Rev. Gén. Bot. **3**: 450. *pl. 18. f. G.* 1891.

FRANCE: Roquehaute, near Béziers, Hérault, *Balansa*, 1866, *Crozals*, 1902; mare de Rigaud near Agde, Hérault, *Crozals*, 1902.

RIELLA COSSONIANA Trab.; Batt. & Trab. Atlas Fl. Alg. **1**: 6. *pl. 2. f. 1–8.* 1886; Rev. Bryol. **14**: 12. *pl.* 1887.

ALGERIA †: El Kreider, Province Oran, *Cosson*, 1854; *Trabut*, 1885.

EXSICC.: Husnot, Hep. Gall. no. 174.

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* Trevisan rejected *Riella* Mont. on account of *Riella* Raf.; Lév.; Orb. Dict. Univ. Hist. Nat. **8**: 488. 1849. This, however, is a *nomen nudum* and is probably a misprint for *Rimella* Raf. Jour. Phys. **89**: 106. 1819.

† Allusions to the occurrence of *Riella Cossoniana* in the Canaries have recently appeared in print (Bot. Tidsskrift, **24**: 327. 1902; Rev. Bryol. **29**: 110. 1902), but it is possible that these refer to *Riella affinis*, described below as new.

RIELLA HELICOPHYLLA (Bory & Mont.) Mont. Ann. Sci. Nat. III. **18**: 12. 1852; Syll. Gen. Sp. Crypt. 94. 1856.

Duriaea helicophylla Bory & Mont. Compt. Rend. Hebd. Acad. Sci. **16**: 1116. 1843; Ann. Sci. Nat. III. **1**: 229. 1844. G. L. & N. Syn. Hep. 593. 1846. Mont.; Bory & Durieu, Expl. Sci., Algérie, Bot. *pl. 34*. 1846–49.

ALGERIA: Province Oran, *Durieu*, *Trabut*.

EXSICC.: Husnot, Hep. Gall. no. 172.

RIELLA NOTARISII (Mont.) Mont. Ann. Sci. Nat. III. **18**: 12. 1852; Syll. Gen. Sp. Crypt. 94. 1856.

Sphaerocarpus Notarisii Mont.; De Not. Mem. R. Accad. Torino, II. **1**: 343. *f. d. 1–8*. 1839.

Duriaea Notarisii Bory & Mont. Compt. Rend. Hebd. Acad. Sci. **16**: 1116. 1843; Ann. Sci. Nat. III. **1**: 229. 1844. G. L. & N. Syn. Hep. 593. 1846.

SARDINIA: near Pula, *De Notaris*, 1834.

GREECE: Phalerus, *Chaboisseau*, *fide* Stephani.

RIELLA PARISII Gottsche; G. & R. Hep. Eur. no. 375. 1867. [Illust.] Leitgeb, Untersuch. Hep. **4**: 76. *pl. 7. f. 17*. 1879. Stephani, Bull. Herb. Boiss. **7**: 661. 1899.

Riella Clausoni[*s*] Letourneux; Husnot, Hepaticologia Gallica, 87. *pl. 12. f. 151*. 1881. Batt. & Trab. Atlas Fl. Alg. **1**: 13. *pl. 8*. 1886. Trab. Rev. Gén. Bot. **3**: 452. 1891.

ALGERIA: Maison-Carrée, etc., near Algiers, *Clauson*, *Paris*, *Trabut*.

EXSICC.: G. & R. Hep. Eur. no. 375; Husnot, Hep. Gall. no. 121.

RIELLA PAULSENII Porsild, Bot. Tidsskrift, **24**: 323–327. *f. 1–3*. 1902.

TURKESTAN: Bokhara, *Paulsen*, 1898.

RIELLA REUTERI Mont. Ann. Sci. Nat. III. **18**: 12. 1852. Hofmeister, Bericht. Verh. Kgl. Sächs. Gesellsch. Wiss. 1854: 92–95. *pl. 4*.

SWITZERLAND: near Geneva, *Reuter*, 1851.

In describing *Riella Paulsenii*, the first species of the genus known to occur outside of the Mediterranean region, Porsild expresses the surmise that the distribution of the genus may prove to be still more widely extended, which is well verified by the known existence at the present time of three specimens of *Riella* collected within the boundaries of the United States. One of these, strangely enough, was collected by Schott as long ago as 1855, but has remained unstudied and unnoted in literature. In April, 1902, western Texas, the region from which Schott's specimens came, was visited by Professors F. S. Earle and S. M. Tracy, who secured further specimens which we consider the type of the well-marked species described below:

Riella Americana sp. nov.

Erect or ascending, 10–30 mm. high, simple or more commonly 1–4 times furcate: axis elliptical in section, 0.2–0.8 mm. wide, mostly 6–10 cells thick, root-hairs borne only on the basal parts and usually few: wing 2–5 mm. broad, rounded-falciform at apex, slightly undulate-crisped, subentire or erose, tapering toward the base and commonly deficient below the first dichotomy; cells near the axis about 60 μ in greatest diameter, those near the margin about 40 μ: scales few, small, 0.2–0.6 mm. long, linguiform and obtuse or irregularly lanceolate and subacute, those near the growing apex usually intermingled with multicellular gemmae: gemmae trichomic in origin, soon oblong or orbicular-oblong in outline, showing later a median constriction and becoming finally panduriform and subspatulate: dioicous: antheridia about 0.36 × 0.16 mm., sometimes as many as 75 (including empty loculi) in a single elongated marginal series: ♀ gametophyte, or each of its branches, maturing for the most part 3–12 sporogonia in acropetal order: involucres smooth, ellipsoidal-ovoid or at full maturity subglobose-ovoid, 1.4–1.8 mm. × 0.8–1.2 mm., narrowed rather gradually to the truncate or slightly pointed subpapillose orifice: capsule globose, 0.8–1 mm. in diameter, seta about 0.2 mm. long, mostly a trifle shorter than the ovoid-conic foot: spores dark-brown, 100–130 μ in maximum diameter (spines included); outer face bearing numerous sometimes curved spines 10–24 μ long, with dilated apices, these spines more or less connected by radiating basal membranes forming irregular reticulations; inner faces bearing conical, non-capitate spines, 3–6 μ long, with basal membranes obsolescent or entirely wanting. (*Pl. 11; pl. 12, f. 21, 22*).

Limpia Cañon, Texas, F. S. Earle and S. M. Tracy, April 25, 1902, no. 251; this, the type specimen, is deposited in the her-

barium of the New York Botanical Garden. The plants are said by Professor Earle to have been found in a pool headed by a small waterfall, forming mats on rocks and stones which were covered by 10–60 cm. of water in the dry season. The same species was collected by Schott in 1855, his specimen originating from "Limpia, near its head, Western Texas." His plants, though otherwise agreeing perfectly with those of the more recent collection, are considerably smaller and are mostly unbranched. A *Riella* (in herb. A. W. Evans) was collected by Mr. De Alton Saunders at Brookings, South Dakota, in 1898. The material is scanty and the sporogonia are so immature that the spore-characters cannot be determined. The involucres and scales are similar to those of *R. Americana* and it is quite probable that the species is the same. This South Dakota specimen marks the northern limit in the known distribution of the genus.

Riella Americana is easily distinguished from any of the species hitherto known. Its nearest ally is probably *Riella Battandieri* f. *Gallica*, of southern France, which differs in being monoicous,* in the narrower wing, the smaller spores, with shorter non-capitate spines, etc. Gemmae have not before, to our knowledge, been definitely described in any species of *Riella*, though Goebel (Flora, **77**: 105. 1893) in figuring three young stages of *Riella Battandieri* (?) remarks in a footnote that one of them sprang from a "Zellkörper" while the others came from "Zellfäden." By analogy with what we have observed in *Riella Americana*, it seems very probable that his plant from the "Zellkörper" came from a brood-body of some kind, while those from the "Zellfäden" were derived from spores. The young plants of *Riella Cossoniana*, represented by Trabut in his figures 1 and 2 (*l. c.*), also, with little doubt, originated from gemmae. The gemmiform appendages figured by Trabut on the axis of his *R. Gallica* are of a more doubtful nature. These were not found by Corbière in his recent studies of what he believes to be the same species; possibly they were designed to represent remains of old involucres and sporogonia.

The gemmae of *R. Americana* originate on the axis as trichomic outgrowths, each of about three cells in a single series (*f. 10, 11*) of which the terminal cell is usually the largest. The two

* Corbière, Rev. Bryol. **29**: 111, 113. 1902.

lower cells then divide in the sagittal plane (*f.* *11*) and this this is followed by a division of the terminal cell. The basal cells afterward grow out and divide in such a way as to give the body a free margin throughout its periphery, though it remains attached to the axis for a considerable time by a single cell on its proximal surface. *F.* *13–16* show stages in the subsequent development, *14* being a view of its proximal surface, and *13*, *15* and *16* of its distal, the point of attachment in each case being at *b*. The part which is derived from the base of the original trichome consists soon of cells which are smaller, richer in protoplasm, and capable of more rapid division than those of the part which is derived from the apex of the original trichome. This part of basal origin is more regularly suborbicular in outline than the other. In neither part can an apical cell be pointed out with any certainty. In the earlier stages the whole body seems to be meristematic; later a constriction appears near its middle and the formation of new cells is then the most active in the zone of this constriction. The larger-celled part, derived from the apex or distal end of the initial trichome, becomes at about this time more than one cell thick in its middle and terminal regions and shows papilliform outgrowths, the beginnings of the root-hairs. The smaller-celled portion derived from the base or proximal end of the initial trichome remains only one cell thick except in the isthmus of constriction where it finally, in part at least, becomes two or more cells thick. *F.* *16* shows a well-developed gemma inverted as regards its original relations to the axis of the gametophyte. The edges of the two parts here overlap slightly in the zone of constriction. Later, the isthmus elongates, giving the body a somewhat panduriform or at length subspatulate outline. *F.* *17* shows the outline of a gemma in an older stage, and *f.* *18* a still later development.

Attempts to germinate the spores of the plants collected by Earle and Tracy were made in the autumn and winter of 1902–03. Though the spores were to all appearances mature, the attempts were successful in the case of only a very few spores, which were carried a little beyond the stage represented in our *f.* *21* and *f.* *22*. The germ-tubes in every case observed came out from near the middle of the outer or more spiny face. This tube is first

divided by transverse walls into a single row of several cells, three or four of the terminal of which are then divided by median longitudinal walls. This divided terminal portion by growth and multiplication of its cells becomes ovate or spatulate in outline. In the latest stage that we have been able to see, one somewhat more advanced than that represented in our *f. 21*, the whole body still consists of only one layer of cells. *F. 22* shows in edgewise view the same plant that is shown in *f. 21*. A root-hair is sent out from the spore soon after the emergence of the germ-tubes.

A second species of *Riella*, apparently new, from the Canary Islands, has come to our attention; this we would describe as follows:

Riella affinis sp. nov.

Apparently erect or ascending, becoming prostrate on the subsidence of the water, 6–15 mm. high, densely caespitose, simple or sparingly furcate: axis flattened, 0.1–0.4 mm. wide, mostly thin and flaccid, radicelliferous at base: wing 1–3 mm. broad, rounded or obtusely pointed at apex and falciform, deeply lobed; cells near the axis 45–60 μ in diameter, those near the margin about 30 μ: scales usually inconspicuous, 0.2–0.5 mm. long, linguiform, lanceolate, or linear, obtuse or acute: monoicous: antheridia solitary or in groups of 2–7 in more or less profound marginal sinuses: sporogonia mostly 3–10: involucres ovoid, 8-winged, 1.4–2 mm. long, 1–1.5 mm. wide (incl. wings), much contracted and often subacute at mouth; wings 0.1–0.2 mm. broad, with undulate-sinuate or subentire margin: capsule subglobose, 0.8–1 mm. in diameter, seta 0.1–0.2 mm. long: spores brown, 85–120 μ in maximum diameter (spines included); outer face densely covered with spines 6–15 μ long, their apices mostly truncate, often slightly dilated, occasionally emarginate-bifid, rarely acute, the supporting basal membranes sometimes almost deficient but commonly forming a few imperfect areolae; inner faces with mostly truncate or obtuse spines or warts 3–6 μ high, basal membranes wanting. (*Pl. 12. f. 23–36.*)

On the bank of a reservoir, Tafira, Grand Canary, June, 1897, O. F. Cook (no. 729). We are informed by the collector that the specimens were found partly submerged and partly exposed on a sloping bank.

Riella affinis is allied to the Algerian *R. Cossoniana* Trabut and the central Asian *R. Paulsenii* Porsild, but differs from both in being monoicous and in the much longer spines of the larger

spores. The involucres are less globose and more pointed at the apex than those of *R. Cossoniana*. Judging from two specimens of *R. Cossoniana* collected by Professor Trabut, *R. affinis* has the appearance of being a larger species with broader lamina, though this might not appear from a comparison of the measurements given above with those given by authors for *R. Cossoniana*. Our specimens of *R. affinis* are prostrate and more or less entangled with mud and are so delicate and fragile that it is quite possible that the measurements in the above description may fail to do full justice to the height of the plant. It may be remarked that in occasional capsules the spores though showing a well-developed brown coloration have short spines or papillae much like those of *R. Cossoniana;* such spores are always smaller than is normal for the species and are probably immature or else have ripened under abnormal conditions.

Our experiments in germinating the spores of *Riella affinis* have been more successful than those with the spores of *Riella Americana*, though they were not begun until December, 1902, five and a half years from the date of collection of the specimens. More than half of the spores experimented with germinated in a few days by being placed on a piece of wet filter-paper in a glass dish kept in a moist chamber at ordinary living-room temperatures. The germ-tube in practically all cases emerges, as in *R. Americana*, from the outer or more spiny face of the spore, usually near its middle. The root-hair follows a little later, its lumen remaining continuous with that of the germ-tube. The length of the germ-tube varies exceedingly. Finally, there appears in it a somewhat curved transverse wall with its convexity turned toward the spore. The part above contains most of the starch grains and in the course of time begins to show chlorophyll, cell-divisions meanwhile taking place as described above for *R. Americana*. The length of the germ-tube from the spore-wall to the curved septum has been observed to vary in different cases from 0.02–0.7 mm. One or two root-hairs, in addition to the one which comes from the base of the germ-tube, may spring out later from some part of the filamentous stalk of the young gametophyte. The forms assumed by the young gametophytes are extremely varied and are doubtless determined to a considerable extent by the conditions of

illumination, though no exact investigations were undertaken to demonstrate the influence of light in this matter. The prevailing form, however, while still unistratose, is spatulate, though flabelliform and linear outlines are not uncommon and grotesquely lobed and branched stages are often met with. Linear or ribbon-shaped forms, like that shown in *f. 36*, are especially common when the young plants are from the first well covered with water. Just below the chief growing point *c*, in the stage illustrated by *f. 34*, there are cell divisions in the plane of the paper, which possibly foreshadow the axis or stem, though they may have arisen in this case through changed relations to the light. We have not yet been able to follow the development much beyond this point, but we have grounds for believing that the subsequent history is essentially as described by Goebel (*l. c.*) for young plants of *A. Battandieri* with the exception that the wing is probably more lobed than in that species. In most cases, the development is confined to practically a single plane, though occasionally, as in the case represented by *f. 35*, the wing-lobes show an irregularly spiral arrangement, due perhaps to changed positions in regard to the light.

Explanation of Plates

[The drawings have been prepared by M. A. Howe, chiefly with the aid of a camera lucida.]

PLATE 11. *Riella Americana* Howe & Underw.

1 and 4. ♂ gametophytes, natural size.

2 and 3. ♀ gametophytes, natural size.

5. Terminal portion of a branch of the ♂ gametophyte, with a young branch at the apex, × 11.

6. Terminal portion of a branch of the ♀ gametophyte, × 11.

7. An involucre, with mature sporogonium, × 16.

8. A scale, × 55.

9. Portion of axis near the apex, showing gemmae and scales, × 40. The gemmae are shown at *a* and below; the scales are, in this case, nearer the wing.

10–18. Stages in the development of the gemmae. See text, pp. 219 and 220.

10. A trichome destined to become a gemma, in distal (outer) aspect, × 193.

11. A similar stage in lateral view, × 193.

12–15. Later stages; 12, 13, and 15 in distal aspect, 14 in proximal, × 193; *b*, point of attachment.

16. A more advanced stage inverted as regards its original relations to the axis and as regards the preceding figures, × 193.

17. Outline of a gemma in a later stage, × 55.

18. A young gametophyte derived from a gemma, × 28.

19 and 20. Spores, outer and inner faces, × 305.

Figures 4, 18–20, are drawn from material collected by Schott in 1855; the others from material collected by Earle and Tracy, April, 1902.

PLATE 12

Figs. 21 and 22, *Riella Americana* Howe & Underw.; Figs. 23–36, *Riella affini* Howe & Underw.

21. Germ plant, × 245.

22. Same in edgewise view, × 245.

23. Gametophyte of *Riella affinis*, × 11.

24. Apical portion of another, with involucres and antheridial loculi, × 11.

25 and 26. Involucres, × 16.

27 and 28. Spores, outer and inner faces, respectively, × 330.

29 and 30. Germinating spores, × 55.

31. Germ plant, showing the earlier cell divisions, × 245.

32–36. Various forms assumed by the germ plants, × 55. The principal vegetative point is indicated by *c*. The elongate form represented in Fig. 36 is common when the young plants are well covered with water.